Palaeobiology and behaviour

Sarah Elton
Evolutionary Anthropology Research Group, Department of Anthropology
Durham University
Durham, UK, DH1 3LE
sarah.elton@durham.ac.uk

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Abstract
Palaeobiology, the study of ancient life, gives us a window onto the habits, biology and behaviour of individuals and species that are now extinct. Although extinct species cannot be observed directly, their palaeobiology and behaviour can be inferred from study of the fossil and geological records in combination with knowledge about modern organisms and processes. Palaeobiological reconstructions thus help to shed light on many aspects of ancient lives, including ecology, diet, locomotion, life history, mating systems, biogeography, speciation, extinction and abundance.

Main text
Palaeobiology, the study of ancient life, gives us a window onto the habits, biology and behaviour of individuals and species that are now extinct. Palaeobiological reconstructions help to shed light on many aspects of ancient lives, including ecology, diet, locomotion, life history, mating systems, biogeography, speciation, extinction and abundance. Although these cannot be observed directly, they can be inferred from study of the fossil and geological records in combination with knowledge about modern organisms and processes. Central to these inferences is the concept of 'uniformitarianism', a framework comprising a set of principles and processes that are assumed not to vary over time or from place to place. So, although the lives of many ancient organisms are likely to have been very different to those of their closest modern relatives, we expect that many of the underpinning principles of evolution, divergence, ecology and behaviour have remained constant. As an illustration of this, fundamental biomechanics (governing, for instance, how limbs or jaws work) have probably not changed over time, so our knowledge of functional morphology in living groups can be used alongside data from the fossil record to reconstruct aspects of the biology and behaviour of extinct animals. However, when investigating palaeobiology and behaviour, caution must always be exercised. For example, a morphological feature may not map neatly onto its expected function, as it could have been retained from an ancestor rather than being used actively, or the ecology of an animal could have changed prior to adaptation taking place. Using multiple lines of evidence to build up a picture of palaeobiological and behavioural characteristics in extinct individuals or species is thus always desirable, where possible.

Palaeobiologists use a variety of tools and evidence in their reconstructions. Different types of fossils provide complementary information. Trace (or ichno-) fossils preserve traces of behaviour and activity, such as footprints and burrows. The Laetoli footprints from Tanzania, tracks left in volcanic ash by the hominin *Australopithecus afarensis* or a close relative, are very well-known trace fossils from the primate record, and have provided considerable information about the evolution of bipedalism. Old World monkey footprints, alongside tracks from several other mammalian species,

have also been found at Laetoli. However, body fossils – the remains of the organisms themselves – are the most common type of fossil in the primate record. Usually, only hard tissues such as bones and, especially, teeth are preserved. Exceptionally, soft tissue impressions are found. The most famous primate example of this is seen in 'Ida' (*Darwinius masillae*) from Messel Pit, for which skin and fur contours were fossilised as well as gut contents, which showed that it had just eaten fruit and leaves (Franzen and Wilde 2003).

Body fossils provide a wealth of palaeobiological and behavioural information. Even something as straightforward as calculating the relative number of fossils assigned to a particular species in an assemblage can help to ascertain its abundance during life, although taphonomic factors (the processes leading [or not] to fossilisation and how those fossils then survive to be recovered) must always be considered. Functional and ecological morphological study of the postcranial skeleton can reveal locomotor and postural behaviour, and by extension, habitat preference. Such studies require a modern sample of known taxonomy, locomotor behaviours and habitats to act as a reference set. Although the skeleton also reflects phylogenetic history, adaptations to locomotion and posture can be found in most parts of the postcranium, which is also shaped by behaviour during life (plasticity). The skeletal elements often preserved in the fossil record tend to be non-fleshy (such as hand and foot bones), as well as the more durable epiphyses of long bones; shafts of long bones are often missing because of ante- or post-mortem damage such as predation or trampling. Nonetheless, much of what we know about fossil primate locomotion has come from isolated or fragmentary material, such as elongation of the calcaneus (heel bone) indicating grasping and / or leaping behaviours and an oblong humeral head being correlated with terrestriality. Full or partial skeletons are rare in the fossil record, but when they exist provide detailed insights into primate locomotor evolution. Study of partial skeletons and isolated elements show that the large colobines from Koobi Fora and other African Pleistocene sites were, in some cases, highly terrestrial and exploited open environments, in contrast to the modern African colobines, all forest-living and arboreal. One of the geologically oldest (and partially-articulated) primate skeletons, from Eocene China, assigned to *Archicebus achilles*, shows a combination of anthropoid and tarsier traits; functionally-informative features, including a long leg, robust femoral neck and partially cylindrical femoral head, demonstrate that it was a leaper but not a specialised vertical clinger and leaper, as its forelimb has adaptations (e.g. fairly rounded humeral head, long coronoid process of the scapula) much more typical of a generalised arboreal quadruped (Ni et al. 2013).

Dental enamel is extremely durable, and teeth are the most common elements in the primate fossil record. Much of what we know about primate evolution comes from the detailed study of dentition. Features diagnostic of particular taxa can often be identified on dental material, and many extinct primate species are known and described primarily from teeth, or teeth and jaws. For example, huge primate diversity in the early Oligocene (a period from which relatively few primate fossils are known) was revealed by the discovery in southern China of mainly teeth and jaws assigned to previously unknown strepsirhine species (Ni et al. 2016). Provided the sediments from which fossils were recovered can be dated, palaeobiologists can build up a picture of speciation and extinction in different lineages even with fairly scant evidence that may comprise only a few teeth. Evidence from a small number of teeth (or indeed any taxonomically-assigned fossil) can also transform our understanding of past primate biogeography and distributions, such as the discovery of platyrrhine teeth in Panama that demonstrate Neotropical monkeys dispersed from South to North America in

the early Miocene, millions of years before the continents were connected by land(Bloch et al. 2016).

Extinct primate growth rates and life histories (the critical stages in an animal's life, such as age at weaning, age at first reproduction and lifespan) can be uncovered through the study of dental development. Teeth grow in a predictable and rhythmic fashion, with daily secretions of enamel and dentine being evident microscopically as lines in tooth sections of both modern and fossil teeth. These lines are known as cross-striations in enamel and von Ebner's lines in dentine. Over slightly longer periods, other, accentuated, incremental lines (Retzius lines in enamel and Andresen's lines in dentine) are formed, again in a predictable fashion. Sometimes, Retzius lines are evident on the external surface of a tooth, in which case they are called perikymata. By counting daily increments, it is possible to ascertain the formation time of long-period lines. By combining information from these and daily lines, the length of time it took the tooth crown (and its root) to form can be calculated. This in turn provides some information about the rapidity of growth in an individual, and hence gives clues to its developmental schedule and life history – i.e. whether it reached maturity quickly or slowly. For example, crown formation times in Neanderthals suggest that despite their big brains they grew and reached maturity more rapidly than did modern humans and *Homo heidelbergensis* (Ramirez Rossi and Bermudez de Castro 2004).

Tooth eruption timing is an important part of the same 'life history' jigsaw. In many primates, there is a close relationship between life history pattern and age of eruption of the first molar (M1). Specifically, this is because M1 eruption age is correlated with adult brain weight, which is itself correlated with life history patterns more generally (Smith 1989). In some primates, M1 eruption age is also linked to weaning. In fossil primates, one way to estimate M1 eruption age is to use incremental growth lines of teeth (such as the incisors) that are still developing alongside data, drawn from comparative samples, on the postnatal timing of tooth mineralisation to calculate age at death for specimens with an erupting M1 (Kelley and Smith 2003). Although modern animals show huge variability in eruption timings, applying this technique showed that M1 eruption in the Miocene ape *Afropithecus turkanensis*, from Kenya, fell within the range of chimpanzees and well outside the range of modern large Old World monkeys (Kelley and Smith 2003). More generally, dental development studies demonstrate that by 18 Ma, Miocene apes had life history patterns that broadly corresponded to those in living apes, which show a grade shift from the pattern evident in monkeys (reviewed in Dean 2006). Seasonal and other stresses can also be identified from incremental tooth growth, which can be disrupted by events such as food shortage or illness. Based on highly accentuated Retzius lines, the Pleistocene monkey *Theropithecus oswaldi* from Koobi Fora appears to have experienced episodic stress, possibly related to seasonality and fluctuations in food availability (Macho et al. 1996).

Diets can obviously be reconstructed via the study of fossil teeth, as well as other cranial and skeletal features. The gross morphology of a tooth gives a broad indication of dietary adaptation: insectivores tend to have molar teeth with pointed cusps, frugivores (fruit eaters) have low rounded molars and folivores (leaf eaters) have molars with shearing crests, although form-function relationships in teeth are not always precise (insectivores may have shearing crests for example). Molar shearing crest prominence can be quantified through the use of a 'shearing quotient' which gives an indication of the relative importance of leaves (or insect exoskeletons) in the diet, with

primates that eat these foods having long, sharp crests in contrast to the shorter crests and shallower molar basins of frugivores. Morphological features of the mandible and cranium can also contribute to our understanding of primate diets and feeding behaviours. Alongside its hypsodont (high-crowned) teeth, a grazing adaptation, *T. oswaldi* has a mandible adapted to efficiently chew grasses through a longer moment arm (the distance between the joint and the force) of the masseter muscle (Jablonski 1993). Forces acting on the skull during mastication can also be modelled with techniques such as finite element analysis (FEA), and applied to fossil primates to help understand how diet and morphology might be linked, and hence potentially add to the array of palaeobiological tools already available. Other skeletal traits may also shed light on diet and, particularly, foraging behaviour. The modern *Theropithecus gelada* has a distinctive shuffling gait, used to move short distances during foraging and correlated with distolateral splay in its femur, plus a high opposability of thumb and forefinger (enabling fine plucking motions) and relatively short fingers, both features associated with manual foraging on grass. Similar traits are evident in extinct *Theropithecus* species, providing good evidence that grazing was a characteristic of the clade. However, primate diets are often varied, so dental and other morphology may only provide part of the picture: many primates with dental adaptations broadly indicative of frugivory supplement their diets with leaves, for example. Primate diets are also dynamic, shifting over time and between groups, so analysing stable light isotopes in fossil tooth enamel or examining dental microwear can provide further lines of evidence when reconstructing the diets and behaviours of ancient primates.

Animals 'are what they eat', as the chemical compositions of their bodies are determined by the foods they consume. Information about an individual's diet can therefore be gleaned from stable light isotope analysis of its tissues. Because of their geological ages, most primate fossils contain little if any organic material, so analysis is limited to tooth enamel, which is extremely resistant to diagenetic change (the conversion to rock that occurs when a fossil is formed). The carbon (C) and oxygen (O) isotopes in enamel are most commonly studied, with the ratio of ^{18}O to ^{16}O providing a complex environmental signal and $^{13}C/^{12}C$ ratio indicating the proportion of tropical grasses (C_4) versus non-tropical grasses, tree and shrub products (C_3), or the animals that ate such vegetation, in the diet. Carbon isotope analysis of *T. oswaldi* teeth from Pleistocene eastern Africa indicate that its diet was dominated (sometimes near-exclusively) by tropical grasses (Cerling et al. 2013) although the diet of *T. oswaldi* from Sterkfontein in southern Africa contained around 30% C_3 plants (van der Merwe et al. 2003).

As an animal chews its food, a microscopic amount of dental wear occurs. Successive feeding bouts obliterate previous wear, so dental microwear is often said to record the 'last meal' of an animal (in reality the last few days or weeks of feeding, depending on the abrasiveness of the ingested material). Foods with different properties leave distinctive microwear traces (e.g. pits or scratches) or textures on the teeth, so by establishing these relationships in a comparative modern sample with known diets, the diets of fossil animals can be estimated. Diets of possibly sympatric amphipithecids from the late middle Eocene Pondaung Formation of Burma / Myanmar have been reconstructed based on three separate lines of evidence: dental microwear, molar shearing quotient and body mass estimates (Ramdarshan et al. 2010). Body mass is a fundamental ecological variable that links to many aspects of an animal's life, including locomotion (with larger animals tending to be more terrestrial), life history (with larger animals generally having longer lives and smaller numbers of offspring in which they invest more heavily) and diet. Smaller animals have faster metabolisms, so

generally need to consume relatively more food, or higher quality food, than larger animals. Insectivores are thus usually small (<500 g, known as Kay's threshold) and folivores much larger, with frugivores spanning a wide range of body masses. The body masses of extinct animals are generally estimated based on relationships between morphological dimensions and body masses in similar extant animals. First molar area or length can thus be used to calculate an approximate body mass (as occurred for the Pondaung amphipithecids), but postcranial dimensions (such as femoral head width), when available (and where postcranial material can be attributed to species), often yield more accurate estimates, as the postcranium is load bearing and thus has a more direct relationship with the mass of an animal. The Pondaung amphipithecids were all found to be above 500 g (and therefore unlikely to be insectivorous), with shearing crest quotients indicating frugivory and nut / seed eating, a conclusion reinforced by microwear analysis (Ramdarshan et al. 2010). In contrast, the Eosimiidae species found in the same Formation was probably <500 g, and was reconstructed as a frugivore that supplemented with insects (Ramdarshan et al. 2010).

Insights into mating system and hence socioecology may come from calculation of sexual dimorphism, either size or canine. Many modern primates show considerable dimorphism, although the relationship with behaviour is complex (in general, dimorphic species are assumed to have male-male competition). Large modern Old World monkeys can be particularly size dimorphic, although surprisingly their Pleistocene relatives were less so (Delson et al. 2000), which may reflect slight differences in mating system but also might be because of other factors, such as differing selective pressures on size in the past, or body mass estimation 'noise'. The first evidence of canine sexual dimorphism in primates comes from the early Eocene *Cantius*, an adapiform, with males having considerably larger canines than those seen in females. Examination of crown formation times showed that this dimorphism occurred through the more rapid growth of male canines, rather than bimaturism (where males and females have the same rate of growth but the larger sex grows for longer, as occurs in most sexually dimorphic anthropoids) (Schwartz et al. 2005). Thus, alongside the insights that were gained from observing canine dimorphism in this species, the use of another palaeobiological technique facilitated a greater understanding of evolutionary trends in primate growth and life history. Behaviour can also be investigated using other proxies. For example, strontium isotope evidence (which is a proxy of the geology of the area in which an individual lived) from tooth enamel suggested that *Paranthropus robustus* females were more likely to disperse than males (Copeland et al. 2011).

Archaeology is 'fossilised behaviour' and there is some (albeit increasing) knowledge of the primate archaeological record, helping us to understand technological and cultural behaviour in the past. Published accounts include archaeological records of chimpanzees and macaques that help to reconstruct foraging behaviour, such as long-tailed macaques pounding shellfish (Haslam et al. 2016). Traces of the behaviour of other animals also aid palaeobiological and behavioural reconstruction in primates. For example, predators may leave tooth, claw or even tool marks on their prey, or remains of prey may be contained in coprolites (fossilised faeces). There are several well-documented examples of predation in the primate fossil record, including *Europolemur* at Messel found in the coprolite of an aquatic mammal, another *Europolemur* shaken in half by a crocodilian, raptor hunting of apes including hominins, and numerous carnivore tooth marks on primates across their evolutionary history (reviewed in Meloro and Elton 2012). This helps paint a

picture of primate palaeoecology, which in turn can aid our understanding of palaeobiology and behaviour over time.

See also: Adapiform; Arboreal locomotion; Biogeography and primate biogeography; Body size and scaling; Cultural behaviour; Dental development; Dental variation; Dentition; Diets and nutrition; Evolution of the Hominoidea; Ecological morphology; Environmental stress; Evolution of Neotropical primates; Form/function framework; Gelada (*Theropithecus*); Hominins; Koobi Fora; Life history; Messel Pit; Miocene primates; Oligocene primates; Palaeocene and Eocene primates; Pleistocene primates; Pliocene primates; Sexual dimorphism; Stable isotope ecology.

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